

Genotypic comparisons of chromosomes 01, 04, and 18 from three tetraploid species of *Gossypium* in topcrosses with five elite cultivars of *G. hirsutum* L.

Johnie N. Jenkins  · Jack C. McCarty Jr. · B. Todd Campbell ·
R. W. Hayes · Jixiang Wu · Sukumar Saha · David Stelly

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Abstract Upland cotton, *Gossypium hirsutum* L. is the most widely planted cultivated cotton in the United States and the world. The other cultivated tetraploid species *G. barbadense* L. is planted on considerable less area; however, it produces extra long, strong, and fine fibers which spins into superior yarn. The wild cotton tetraploid species *G. tomentosum* Nuttall ex Seemann, native to the Hawaiian Archipelago also exhibits traits, such as drought tolerance, that would also be desirable to transfer to Upland cotton. Long-term breeding efforts using whole genome crosses between Upland and these species have not been successful in transferring very

many desirable alleles into Upland cotton. Our chromosome substitution lines (CSL) have one chromosome or chromosome arm from an alien species backcrossed into the Upland cotton line, TM-1, via aneuploid technology. Five Upland cultivars were crossed with CS-B01, CS-T01, CS-B04, CS-T04, CS-B18 and CS-T18 and TM-1 the recurrent parent of the CSLs. This provided an opportunity to determine the effects of chromosomes 01, 04, and 18 from the three species in crosses with the five cultivars. Predicted genotypic mean effects of the parents, F₂, and F₃ generations for eight agronomic and fiber traits of importance were compared. The predicted hybrid mean effects for the three chromosomes from each species were different for several of the traits across cultivars. There was no single chromosome or species that was superior for all traits in crosses. Parental and hybrid lines often differed in the effect of a particular chromosome among the three species. The predicted genotypic mean effects for F₂ and F₃, with a few exceptions, generally agree with our previous results for additive and dominance genetic effects of these CSL.

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J. N. Jenkins (✉) · J. C. McCarty Jr. ·
R. W. Hayes · S. Saha
USDA-ARS, P. O. Box 5367, Starkville, MS 39762, USA
e-mail: Johnie.Jenkins@ars.usda.gov

B. T. Campbell
USDA-ARS, Florence, SC 29501, USA

J. Wu
Agronomy, Horticulture and Plant Science Department,
South Dakota State University, Brookings, SD 57007,
USA

D. Stelly
Department of Soil and Crop Sciences, Texas A&M
University, College Station, TX 77843-2474, USA

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Abbreviations

CSL Chromosome substitution line
CS-B Chromosome substitution line from *G. barbadense*

| | |
|-----------|--|
| CS-T | Chromosome substitution line from <i>G. tomentosum</i> |
| GGE model | Genotype and Genotype-by-environment model |

Introduction

Researchers in Upland cotton (*Gossypium hirsutum* L.) have had access to several chromosome substitution lines (CSL) for only a few years; although the principles of cotton cytogenetic behavior, transmission, and inheritance for development of interspecific chromosome substitution lines in cotton were outlined earlier by Endrizzi (1963). The first hypoaneuploid-based backcross substitution of different *G. barbadense* chromosome or chromosome segments were introduced into *G. hirsutum* and released to the general public by Stelly et al. (2005). Additional CSL of select chromosomes from *G. tomentosum* (Nuttall ex Seeman) have been developed by our team, but not released to the general public.

In bread wheat (*Triticum aestivum* L., $2n = 42$) CSL have been effectively used for intraspecific introgression, genetic studies of individual chromosome associated with quantitative traits, and fine mapping of quantitative traits within individual chromosomes (Al-Quadhy et al. 1988; Berke et al. 1992a, b; Campbell et al. 2003, 2004; Kaeppler 1997; Law 1966; Mansur et al. 1990; Shah et al. 1999; Yen and Baenziger 1992; Yen et al. 1997; Zemetra and Morris 1988; Zemetra et al. 1986). Evaluation of a full set of reciprocal CSL between two winter wheat cultivars ‘Wichita’ and ‘Cheyenne’ showed that chromosome 3A from Wichita increased grain yield ~15% when placed in Cheyenne background and 3A from Cheyenne reduced grain yield ~15% when placed in Wichita background (Berke et al. 1992a, b). Further developments of chromosome specific recombinant inbred lines for both chromosomes allowed a much finer dissection of genomic regions associated with 3A from Wichita in Cheyenne background (Campbell et al. 2003, 2004) and 3A from Cheyenne in Wichita background (Mengistu et al. 2012).

The development of CSL for the same chromosome or segment from two tetraploid species of *Gossypium* provided us with the opportunity to compare individual CSLs from these species in crosses with Upland

elite breeding lines. CSLs have been suggested to be effective ways to introgress useful alleles from wild tetraploid species into Upland, *G. hirsutum* L. (Stelly et al. 2005). The contributions of specific chromosomes from different tetraploid species when crossed with modern elite germplasm are of great interest for their ultimate utility in plant breeding. Most research of this type has been with CSL from *G. barbadense* (CS-B) crossed to five cultivars. A summary of useful additive alleles from CS-B lines show specific CS-B chromosomes or chromosome arms have alleles for improvement of lint yield, boll weight, lint percentage, fiber upper half mean length, strength, length uniformity, micronaire, and elongation (Jenkins et al. 2006, 2007, 2012, 2013; Zhang et al. 2014). CSLs for *G. barbadense* and *G. tomentosum* for chromosomes 01, 04, and 18 were the first CSLs we had to use to compare specific chromosomes from the three tetraploid species. Additive and dominance genetic effects data from chromosomes 01, 04, and 18 from *G. barbadense*, *G. tomentosum*, and *G. hirsutum* when crossed with five diverse commercial cultivars are reported in (Jenkins et al. 2017). Genotypic mean effects comparisons of these same chromosomes 01, 04, and 18 from *G. barbadense*, *G. tomentosum*, and *G. hirsutum* when crossed with five diverse commercial cultivars are reported here.

Materials and methods

CSL development

Development of each CSL involved three stages: (1) development of a TM-1 like hypoaneuploid stock that served as the TM-1 like recurrent parent via five or more backcrosses, (2) selective introgression of a *Gossypium* spp. chromosome or segment per line to create a monosome substitution stock, also involving five generations of backcrossing, and (3) recovery of the euploid, disomic substitution line, by inbreeding, (Stelly et al. 2005). This process is facilitated by the differential transmission of the hypoaneuploidy of the gametophytes. Transmission of hypoaneuploidy through the ovule parent is common (up to 50%); whereas, transmission is totally lacking, or very rare, through the pollen for all whole-chromosome and most large-segment deletions. With a rough estimate

of 30,000 genes in the cotton genome, we can estimate each of the monosomes-derived CSL carries an average of 1000 or more genes from the introgressed species. According to random probability, we should expect about five-sixths of the difference between a CSL and TM-1 the backcross parent to be due to the substituted chromosome, and the remaining one-sixth due to remnant alien species in nonhomologous chromosomes that was inadvertently retained during backcrossing and inbreeding (Stelly et al. 2005).

Materials and field experiments

Five elite cultivars of Upland cotton were selected from the germplasm of major cotton seed breeding companies in the USA, ['Deltapine 90' (DP 90 PVP 8100143), developed by Delta and Pine Land Co. (Scott, MS); 'Sure-Grow 747' (SG 747 PVP 9800118), developed by Sure-Grow Co. (Center, AL); 'Phytogen 355' (PSC 355 PI 612974), developed by Mississippi Agriculture and Forestry Experiment Station (Mississippi State, MS and licensed to Phytogen Seeds (Indianapolis, IN); 'Stoneville 474' (ST 474 PVP 9400152), developed by Stoneville Pedigreed Seeds; and 'Fibermax 966' (FM 966 PVP 200100209), developed in Australia where it was called 'Sicala 40' and marketed in the United States by Bayer Crop Science FiberMax division]. These five parents were crossed as females with three CS-B lines (CS-B01, CS-B04, and CS-B18), three CSL from *G. tomentosum* (CS-T) lines (CS-T01, CS-T04, and CS-T18), and TM-1 the recurrent parent of the CSL. The CS-B lines were released by Stelly et al. (2005) and the CS-T lines have not been released. The TM-1 crosses provide the comparisons for *G. hirsutum* chromosomes 01, 04, and 18. Pedigrees for the five cultivars were examined and they are fairly diverse as would be expected considering they each came from a different breeding program (Bowman et al. 2006; Calhoun et al. 1994, 1997).

Entries (12 parents and 35 crosses) were grown in single-row plots 12 m long with rows spaced 97 cm and plants spaced 10 cm apart within rows (total 120 plants per row), and evaluated for yield and fiber quality. Planting pattern was two rows planted with one row skipped at Mississippi State, MS and solid planted at Florence, SC. Experiments were conducted in three environments in 2010 and two environments

in 2011. In 2010, F₂ seed and parents were planted and in 2011 F₃ seed and parents were planted. Environments 1, 2, and 4 were on the plant science research farm at Mississippi State, MS (33.4°N, 88.8°W). Genotypes were planted in a Leeper silty clay loam (fine smectitic, non-acid thermic Vertic Epiaquepts) soil type for environments 1 and 4; in Marietta loam (fine-loamy siliceous, active Fluvaquent Eutrudepts) soil for environment 2. Environments 3 and 5 were on the Clemson Pee Dee Research and Education Center near Florence, SC. (34.1°N, 79.4°W), in a Norfolk loamy sand (fine-loamy, kaolinitic, thermic Typic Kandiudults) soil. Planting dates were 12 May, 2010, 13 May, 2010, and 16 May, 2011 at Mississippi State, MS and were 18 May, 2010 and 16 May, 2011 at Florence, SC. A randomized complete block design with four replications was used in each environment.

Entries were grown using standard agronomic practices, and insects were managed using University-recommended practices. Prior to machine harvest a 25-boll random sample was hand-collected in each plot to determine lint percent (LP), boll weight (BW), and fiber quality. Lint yield (LY) was calculated from plots harvested with a commercial cotton picker modified for plot harvesting and weighing. Fiber samples were sent to STARLAB, Knoxville, TN, for High Volume Instrument (HVI[®]) fiber measurements; fiber upper half mean length (UHM); fiber length uniformity (UI); fiber strength (STG); fiber elongation (EL); and fiber micronaire (MIC).

Data analysis

In this study, we used a linear mixed model including genotype and genotype-by-environment interaction effects (GGE model) and we report genotypic mean effects and their comparisons among these parents and hybrids in two generations. With the use of GGE model, we treated different entries as different genotypes and the linear model used in this study was:

$$y_{hij} = \mu + E_h + G_i + GE_{hi} + B_{j(h)} + e_{hij}$$

where y_{hij} is the observed value for genotype i under environment h with block j ; μ is a population mean; E_h is an environmental effect; G_i is a genotypic effect; GE_{hi} is an interaction effect between genotype i and environment h ; $B_{j(h)}$ is a block effect within an environment; and e_{hij} is a random error.

In order to evaluate the contribution of each component to the phenotypic variance, we treated each effect as a random effect and used the minimum norm quadratic unbiased estimation approach (Rao 1971; Zhu 1989), to estimate variance components and predict all effects (Wu 2014; Wu et al. 2010, 2014; Zhu 1993). A randomized tenfold jackknife technique was applied to estimate standard error for parameters of interest, and then an approximate *t* test with degrees of freedom of nine was used to test significance for each parameter (Wu et al. 2012, 2013). All data analyses were conducted using the minque R package (R Core Team 2014; Wu 2014).

We made three types of comparisons among means. A general predicted mean effects comparison among parents, a predicted mean effects comparison per chromosome, which allowed the comparison of the effects of *G. barbadense*, *G. tomentosum*, and *G. hirsutum* chromosomes, and a comparison of predicted hybrid effects.

Results

Variance components

Genotypic by environment variances were significant only for boll weight (BW), lint yield (LY), fiber elongation (EL), and Micronaire (MIC); however, these $G \times E$ variances were small compared to the main effect variances. The genotypic variance was larger than environmental variances for LP and fiber strength (STG) indicating that selections for these traits should be less affected by environment than for other traits. The two variances were about equal for

LY, and environmental variance was larger than genotypic variance for BW, fiber upper half mean (UHM), uniformity index (UI), EL, and MIC. Genotype variance for UHM is often larger than environmental variances, but it was not in these studies. Predicted environmental means show that the environments were significant and the $G \times E$ interaction variances were small (Table 1).

Parent genotypic mean effects

Table 2 provides the predicted genotypic effects as deviations from the population mean for TM-1, the six CSL, and the five elite commercial cultivars for agronomic and fiber quality traits. Predicted genotypic effects for LP and LY were lower for TM-1 and all CSL than for cultivars. Bolls of TM-1 were heavier than any CSL or cultivar. Among the cultivars tested, FM 966 had the heaviest bolls. SG 747 and ST 474 had the highest LY among all genotypes evaluated. CS-B01, CS-B04, CS-T04, and FM 966 produced the longest UHM fiber length. The strongest fibers were produced by cultivars PSC 355 and FM 966. PSC 355 had the greatest fiber EL and CS-B01 had the lowest MIC.

Chromosome substitution lines among *G. hirsutum*, *G. barbadense*, and *G. tomentosum*, were compared for each individual chromosome in isochromosomal TM-1 (*G. hirsutum*) genetic background to compare the effect of each of the three species. Means for TM-1, CS-B and CS-T lines (with error bars at 95% confidence intervals) are plotted as deviations from the population mean with TM-1 set as zero (with error bars at 95% confidence intervals) in Figs. 1, 2 and 3.

Table 1 Variance components for agronomic and fiber traits expressed as proportion of total variances

| Variance | LP (%) | BW (G) | LY (kg ha ⁻¹) | UHM (mm) | UI (%) | STG (kN m kg ⁻¹) | EL (%) | MIC |
|----------------------|---------|---------|---------------------------|----------|---------|------------------------------|----------|---------|
| V_G/V_p | 0.539** | 0.267** | 0.181** | 0.1679** | 0.107** | 0.349** | 0.113** | 0.230** |
| V_E/V_p | 0.342** | 0.413** | 0.205** | 0.5024** | 0.412** | 0.261** | 0.548** | 0.451** |
| $V_{G \times E}/V_p$ | 0.000ns | 0.054** | 0.076** | 0.0165ns | 0.018ns | 0.011ns | 0.016* | 0.066** |
| V_B/V_p | 0.001ns | 0.001ns | 0.023** | 0.0122** | 0.019* | 0.035** | 0.099 ns | 0.007** |
| V_{res}/V_p | 0.118** | 0.266** | 0.515** | 0.3011** | 0.445** | 0.345** | 0.224** | 0.245** |
| Total V_p | 7.708 | 0.364 | 84,532 | 1.4366 | 1.667 | 770.111 | 0.517 | 0.236 |

V_G genotypic variance; V_E environmental variance; $V_{G \times E}$ genotypic by environmental variance; V_B block variance within environments; V_{res} residual variance; V_p phenotypic variance

** Significantly different than zero at 0.01 probability level

Table 2 Population mean, minimum (Min), and maximum (Max) values, and predicted parental genotypic mean effects and standard errors as deviations from the population mean for agronomic and fiber traits

| Entry | LP \pm SE (%) ^a | BW \pm SE (G) | LY \pm SE (kg ha ⁻¹) | UHM \pm SE (mm) | UI \pm SE (%) | STG (kN m kg ⁻¹) | ELO \pm SE (%) | MIC \pm SE |
|--|------------------------------|------------------|------------------------------------|-------------------|------------------|------------------------------|------------------|------------------|
| Population mean, minimum and maximum genotypic means and genotypic effects | | | | | | | | |
| Pop mean | 38.28 | 5.07 | 1001 | 28.2 | 83.4 | 324.8 | 7.04 | 4.99 |
| Min | 31.79 | 4.30 | 591 | 26.4 | 82.1 | 283.2 | 6.62 | 3.93 |
| Max | 44.55 | 5.57 | 1217 | 28.7 | 84.2 | 378.6 | 7.90 | 5.69 |
| Min effect | -6.49 | -0.77 | -411 | -1.82 | -1.31 | -41.6 | -0.42 | -1.06 |
| Max effect | 6.26 | 0.50 | 216 | 0.54 | 0.79 | 53.9 | 0.86 | 0.69 |
| Predicted parental genotypic effects | | | | | | | | |
| TM-1 | -4.16 \pm 0.09 | 0.50 \pm 0.02 | -149 \pm 19 | -0.03 \pm 0.06 | 0.22 \pm 0.07 | -11.6 \pm 1.8 | -0.14 \pm 0.03 | -0.06 \pm 0.02 |
| CS-B01 | -6.20 \pm 0.09 | -0.59 \pm 0.04 | -367 \pm 15 | 0.30 \pm 0.04 | 0.49 \pm 0.04 | -17.3 \pm 0.9 | 0.05 \pm 0.03 | -1.06 \pm 0.03 |
| CS-T01 | -1.01 \pm 0.07 | -0.77 \pm 0.02 | -158 \pm 17 | -1.82 \pm 0.07 | -1.01 \pm 0.08 | -9.6 \pm 2.1 | 0.23 \pm 0.04 | 0.20 \pm 0.02 |
| CS-B04 | -3.72 \pm 0.09 | 0.32 \pm 0.04 | -248 \pm 16 | 0.54 \pm 0.06 | -0.24 \pm 0.07 | -41.6 \pm 1.1 | -0.33 \pm 0.02 | -0.18 \pm 0.02 |
| CS-T04 | -6.49 \pm 0.10 | 0.19 \pm 0.02 | -174 \pm 17 | 0.46 \pm 0.05 | 0.44 \pm 0.07 | -7.4 \pm 2.0 | -0.03 \pm 0.03 | -0.04 \pm 0.01 |
| CS-B18 | -3.34 \pm 0.08 | -0.09 \pm 0.04 | -269 \pm 19 | -0.70 \pm 0.04 | -0.87 \pm 0.06 | -0.3 \pm 1.4 | 0.41 \pm 0.03 | 0.69 \pm 0.02 |
| CS-T18 | -5.08 \pm 0.08 | -0.53 \pm 0.02 | -411 \pm 12 | -0.29 \pm 0.06 | -1.31 \pm 0.09 | -7.1 \pm 1.7 | -0.35 \pm 0.04 | 0.04 \pm 0.01 |
| DP 90 | 0.80 \pm 0.11 | -0.35 \pm 0.02 | 91 \pm 15 | -0.43 \pm 0.06 | -0.57 \pm 0.07 | 1.8 \pm 1.3 | -0.02 \pm 0.03 | -0.02 \pm 0.02 |
| SG 747 | 5.99 \pm 0.11 | 0.16 \pm 0.03 | 216 \pm 21 | -0.34 \pm 0.08 | 0.61 \pm 0.08 | -24.0 \pm 1.4 | 0.27 \pm 0.04 | 0.14 \pm 0.02 |
| PSC 355 | 2.97 \pm 0.10 | -0.55 \pm 0.02 | 19 \pm 25 | -0.94 \pm 0.05 | 0.48 \pm 0.06 | 17.5 \pm 1.6 | 0.86 \pm 0.04 | 0.24 \pm 0.02 |
| ST 474 | 6.26 \pm 0.15 | -0.49 \pm 0.02 | 156 \pm 23 | -0.89 \pm 0.08 | -0.32 \pm 0.08 | -18.6 \pm 1.5 | -0.07 \pm 0.03 | 0.12 \pm 0.02 |
| FM 966 | 3.15 \pm 0.06 | 0.28 \pm 0.04 | 33 \pm 20 | 0.25 \pm 0.05 | 0.79 \pm 0.07 | 53.9 \pm 3.0 | -0.42 \pm 0.03 | -0.24 \pm 0.03 |

BW boll weight in grams, LY lint yield in kg ha⁻¹, Upper half mean in mm, Uniformity index in Percentage, STG Strength in kN m kg⁻¹, EL Elongation in percentage, MIC Micronaire values

^a Lint in percentage

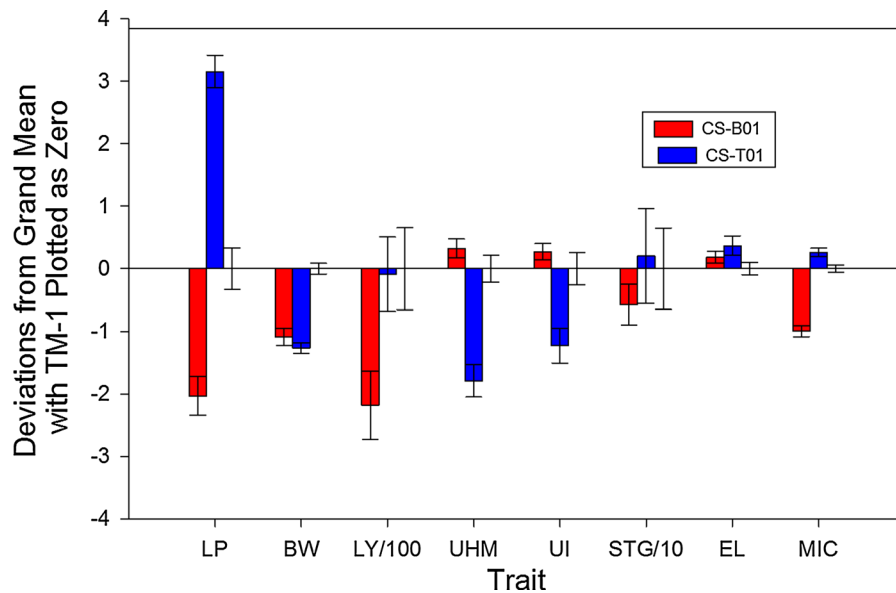


Fig. 1 Chromosome 01 predicted parental genotypic mean effects plotted as deviations from population mean with TM-1 means plotted as zero. Error bars show 95% confidence

intervals. *LP* lint %; *BW* boll wt.; *LY/100* lint yield/100; *UHM* fiber upper half mean length; *UI* fiber length uniformity; *STG/10* fiber strength/10; *EL* fiber elongation; *MIC* Micronaire

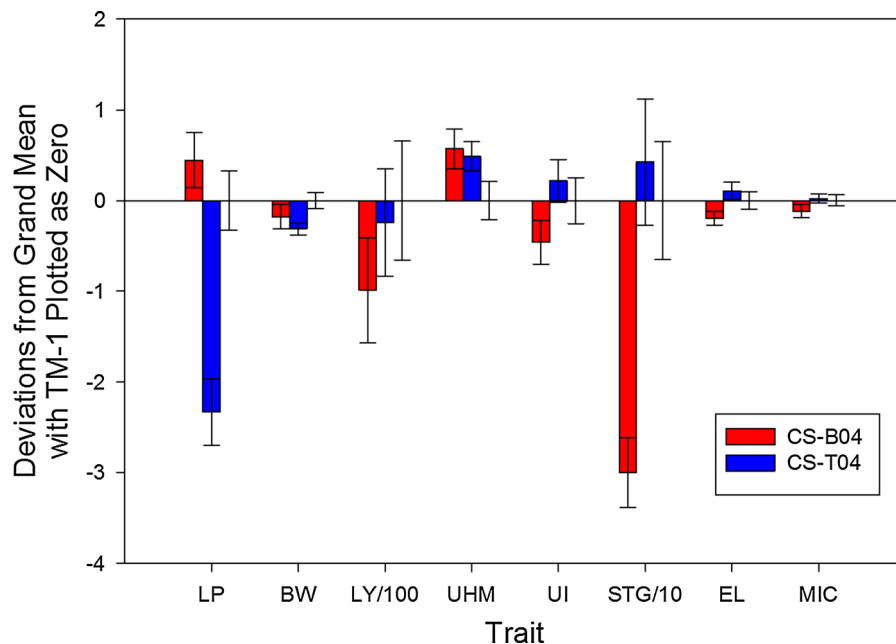


Fig. 2 Chromosome 04 predicted parental genotypic mean effects plotted as deviations from population mean with TM-1 means plotted as zero. Error bars show 95% confidence intervals. See Fig. 1 for trait identification

For chromosome 1, the *barbadense* substitution line (CS-B01) decreased LP, BW, LY, and MIC. The *tomentosum* substitution line (CS-T01) increased LP

and MIC while decreasing both UHM length and UI. Relative to TM-1, chromosome 1 substitutions had little effect on STG. Interestingly, CS-B01 and CS-

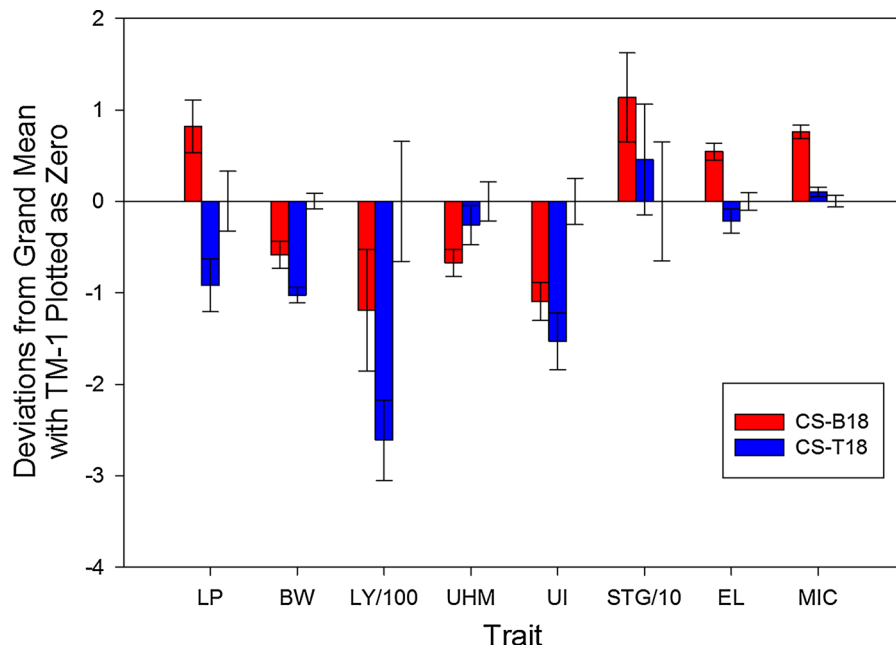


Fig. 3 Chromosome 18 predicted parental genotypic mean effects plotted as deviations from population mean with TM-1 means plotted as zero. Error bars show 95% confidence intervals. See Fig. 1 for trait identification

T01 had opposite effects as compared to TM-1 on LP and MIC (Fig. 1).

For chromosome 4, the *barbadense* substitution line (CS-B04) significantly decreased LY and fiber STG while increasing UHM length. The *tomentosum* substitution line (CS-T04) significantly decreased LP, decreased BW, and increased UHM length. Relative to the *hirsutum* (TM-1) chromosome, effects of both CSLs were negligible for LY, UHM, UI, EL, and MIC. CS-B04 and CS-T04 substitution lines had opposite effects as compared to TM-1 for LP and fiber STG (Fig. 2).

For chromosome 18, the *barbadense* substitution line (CS-B18) significantly increased LP, EL, and MIC while decreasing BW, UHM length, and UI. The *tomentosum* substitution line (CS-T18) significantly decreased LP, BW, LY, and UI. Chromosome 18 substitution lines had opposite effects as compared to TM-1 for LP (Fig. 3).

Predicted genotypic effects of chromosome 01 hybrids

F₂ and F₃ predicted hybrid mean effects with the five cultivars are shown in Table 3 for all traits. CS-B01/

DP 90 hybrids had lower LP, heavier bolls, more LY, longer UHM, more uniform fibers, and lower MIC than CS-T01/DP 90 hybrids. STG was lower in F₂ but greater in F₃ CS-B01 hybrids than CS-T01 hybrids. CS-B01/SG 747 hybrids had heavier bolls, longer UHM length, better UI, and lower MIC; whereas CS-T01/SG 747 F₂ hybrids had greater LP, higher LY, and stronger fiber STG. CS-B01/PSC 355 F₂ hybrids had heavier BW, greater LY, greater fiber UHM length, UI, STG, and lower MIC. LY, UHM and STG of F₃ hybrids of CS-B01 were not in agreement with F₂ hybrids. CS-T01/PSC 355 F₂ hybrids had greater LP in F₂ and F₃ hybrids and greater LY. CS-T01/ST 474 F₂ hybrids had greater LP, heavier BW, and higher LY; whereas CS-B01 hybrids had longer UHM length and greater UI with a lower MIC. CS-T01/FM 966 F₂ hybrids had greater LP than CS-B01 hybrids; whereas CS-B01 hybrids had lower MIC. LP of the CSL's and TM-1 was less than the five cultivars.

Predicted genotypic effects of chromosome 04 hybrids

F₂ and F₃ hybrid mean effects with the five cultivars are shown for all traits in Table 4. CS-B04/DP 90 F₂

Table 3 Comparison of predicted F₂ and F₃ mean effects and standard errors for eight traits (lint in percentage) for five cultivar crosses with Chromosome 01, expressed as deviations from population mean

| Male parent | Pop mean | DP90 Mean \pm SE | SG747 Mean \pm SE | PSC355 Mean \pm SE | ST474 Mean \pm SE | FM966 Mean \pm SE |
|-------------|----------|-----------------------|------------------------|-------------------------|------------------------|------------------------|
| LP | 38.28 | | | | | |
| 2010 | | | | | | |
| TM-1 | | -0.57 ± 0.05 | 0.63 ± 0.15 | -0.55 ± 0.08 | 1.19 ± 0.06 | 0.07 ± 0.04 |
| CS-B01 F2 | | -1.58 ± 0.11 | 0.64 ± 0.19 | -0.97 ± 0.16 | 0.92 ± 0.13 | -0.07 ± 0.11 |
| CS-T01 F2 | | 0.57 ± 0.11 | 1.32 ± 0.13 | 0.90 ± 0.06 | 2.29 ± 0.11 | 0.88 ± 0.10 |
| 2011 | | | | | | |
| TM-1 | | -0.70 ± 0.09 | 0.09 ± 0.08 | -0.43 ± 0.07 | 0.39 ± 0.09 | 0.27 ± 0.08 |
| CS-B01 F3 | | -1.34 ± 0.05 | 0.58 ± 0.15 | -0.41 ± 0.08 | -0.46 ± 0.14 | -0.13 ± 0.10 |
| CS-T01 F3 | | -0.53 ± 0.07 | 0.61 ± 0.07 | -0.21 ± 0.11 | 0.93 ± 0.12 | 0.56 ± 0.14 |
| BW | 5.07 | | | | | |
| 2010 | | | | | | |
| TM-1 | | 0.41 ± 0.02 | 0.20 ± 0.03 | 0.09 ± 0.03 | 0.17 ± 0.02 | 0.75 ± 0.04 |
| CS-B01 F2 | | -0.12 ± 0.02 | 0.13 ± 0.03 | -0.17 ± 0.03 | -0.24 ± 0.02 | 0.33 ± 0.03 |
| CS-T01 F2 | | -0.26 ± 0.03 | 0.02 ± 0.04 | -0.43 ± 0.02 | -0.35 ± 0.02 | 0.29 ± 0.03 |
| 2011 | | | | | | |
| TM-1 | | 0.22 ± 0.03 | 0.15 ± 0.02 | 0.09 ± 0.03 | 0.09 ± 0.06 | 0.60 ± 0.03 |
| CS-B01 F3 | | 0.03 ± 0.04 | -0.05 ± 0.02 | -0.13 ± 0.03 | -0.15 ± 0.04 | 0.02 ± 0.04 |
| CS-T01 F3 | | -0.30 ± 0.04 | -0.19 ± 0.06 | -0.25 ± 0.04 | -0.19 ± 0.05 | 0.21 ± 0.05 |
| LY | 1001 | | | | | |
| 2010 | | | | | | |
| TM-1 | | 80 ± 22 | 235 ± 26 | 70 ± 33 | 121 ± 27 | 21 ± 0.05 |
| CS-B01 F2 | | 153 ± 17 | 7 ± 25 | 181 ± 21 | -9 ± 29 | 21 ± 0.35 |
| CS-T01 F2 | | -39 ± 18 | 221 ± 29 | 57 ± 27 | 84 ± 12 | 16 ± 0.05 |
| 2011 | | | | | | |
| TM-1 | | -10 ± 19 | -3 ± 13 | -120 ± 24 | 50 ± 20 | 9 ± 0.00 |
| CS-B01F3 | | 5 ± 22 | -83 ± 10 | -121 ± 11 | -5 ± 13 | 29 ± 0.99 |
| CS-T01 F3 | | -88 ± 17 | 38 ± 16 | -57 ± 24 | 68 ± 22 | 25 ± 0.01 |
| UHM | 28.2 | | | | | |
| 2010 | | | | | | |
| TM-1 | | 0.06 ± 0.06 | 0.02 ± 0.04 | 0.02 ± 0.06 | -0.40 ± 0.07 | 0.60 ± 0.08 |
| CS-B01 F2 | | 0.58 ± 0.06 | 0.36 ± 0.10 | 0.46 ± 0.05 | -0.02 ± 0.04 | 0.78 ± 0.08 |
| CS-T01 F2 | | -0.39 ± 0.06 | -0.43 ± 0.06 | -0.71 ± 0.05 | -1.09 ± 0.08 | -0.20 ± 0.07 |
| 2011 | | | | | | |
| TM-1 | | 0.02 ± 0.06 | 0.02 ± 0.11 | 0.18 ± 0.06 | -0.09 ± 0.07 | 0.20 ± 0.05 |
| CS-B01 F3 | | 0.64 ± 0.06 | -0.11 ± 0.04 | -0.47 ± 0.09 | -0.14 ± 0.07 | 0.05 ± 0.04 |
| CS-T01 F3 | | -0.29 ± 0.06 | -0.68 ± 0.12 | -0.42 ± 0.07 | -0.76 ± 0.05 | 0.07 ± 0.11 |
| UI | 83.4 | | | | | |
| 2010 | | | | | | |
| TM-1 | | -0.18 ± 0.09 | 0.28 ± 0.06 | 0.58 ± 0.06 | -0.03 ± 0.07 | 0.42 ± 0.08 |
| CS-B01 F2 | | 0.06 ± 0.05 | 0.56 ± 0.13 | 0.80 ± 0.07 | 0.26 ± 0.05 | 0.20 ± 0.09 |
| CS-T01 F2 | | -0.39 ± 0.04 | 0.36 ± 0.07 | 0.11 ± 0.04 | -0.59 ± 0.09 | 0.13 ± 0.03 |

Table 3 continued

| Male parent | Pop mean | DP90 Mean \pm SE | SG747 Mean \pm SE | PSC355 Mean \pm SE | ST474 Mean \pm SE | FM966 Mean \pm SE |
|-------------|----------|-----------------------|------------------------|-------------------------|------------------------|------------------------|
| 2011 | | | | | | |
| TM-1 | | -0.14 ± 0.09 | 0.04 ± 0.04 | 0.12 ± 0.06 | 0.21 ± 0.07 | 0.09 ± 0.06 |
| CS-B01 F3 | | 0.17 ± 0.10 | -0.10 ± 0.07 | 0.22 ± 0.05 | 0.15 ± 0.06 | -0.13 ± 0.10 |
| CS-T01 F3 | | -0.56 ± 0.09 | -0.27 ± 0.05 | -0.03 ± 0.13 | -0.48 ± 0.06 | -0.11 ± 0.10 |
| STG | 324.8 | | | | | |
| 2010 | | | | | | |
| TM-1 | | 8.8 ± 1.2 | -11.5 ± 1.8 | -2.7 ± 1.3 | -7.8 ± 1.7 | 30.9 ± 1.0 |
| CS-B01 F2 | | 0.0 ± 1.3 | -22.5 ± 1.6 | 10.9 ± 1.3 | -12.4 ± 1.0 | 24.0 ± 2.3 |
| CS-T01 F2 | | 0.8 ± 1.6 | -10.6 ± 2.1 | 3.9 ± 1.4 | -12.8 ± 1.3 | 24.1 ± 2.5 |
| 2011 | | | | | | |
| TM-1 | | 9.7 ± 2.0 | -16.2 ± 0.9 | -2.6 ± 2.4 | -4.6 ± 2.9 | 30.4 ± 1.8 |
| CS-B01 F3 | | 0.5 ± 1.5 | -25.4 ± 2.0 | -2.5 ± 2.3 | -9.2 ± 1.7 | 23.5 ± 2.5 |
| CS-T01 F3 | | -10.5 ± 1.2 | -11.4 ± 1.7 | 6.6 ± 1.3 | -9.6 ± 2.1 | 24.3 ± 1.8 |
| EL | 7.04 | | | | | |
| 2010 | | | | | | |
| TM-1 | | -0.11 ± 0.03 | -0.21 ± 0.03 | 0.30 ± 0.03 | -0.17 ± 0.03 | -0.29 ± 0.02 |
| CS-B01 F2 | | 0.00 ± 0.02 | 0.27 ± 0.04 | 0.54 ± 0.03 | -0.09 ± 0.06 | -0.37 ± 0.04 |
| CS-T01 F2 | | -0.04 ± 0.06 | 0.16 ± 0.03 | 0.54 ± 0.03 | 0.09 ± 0.04 | -0.28 ± 0.04 |
| 2011 | | | | | | |
| TM-1 | | -0.04 ± 0.02 | 0.05 ± 0.04 | -0.01 ± 0.06 | -0.06 ± 0.03 | -0.13 ± 0.03 |
| CS-B01 F3 | | -0.03 ± 0.02 | 0.15 ± 0.03 | 0.12 ± 0.04 | -0.14 ± 0.03 | -0.16 ± 0.02 |
| CS-T01 F3 | | -0.01 ± 0.05 | 0.22 ± 0.03 | 0.44 ± 0.04 | 0.11 ± 0.03 | -0.04 ± 0.03 |
| MIC | 4.99 | | | | | |
| 2010 | | | | | | |
| TM-1 | | -0.06 ± 0.02 | -0.19 ± 0.03 | 0.07 ± 0.03 | 0.07 ± 0.03 | 0.09 ± 0.02 |
| CS-B01 F2 | | -0.35 ± 0.02 | -0.29 ± 0.04 | -0.26 ± 0.02 | -0.42 ± 0.03 | -0.48 ± 0.02 |
| CS-T01 F2 | | -0.15 ± 0.02 | -0.06 ± 0.03 | 0.13 ± 0.02 | 0.05 ± 0.02 | 0.09 ± 0.02 |
| 2011 | | | | | | |
| TM-1 | | -0.03 ± 0.02 | 0.05 ± 0.03 | 0.08 ± 0.02 | -0.12 ± 0.03 | 0.01 ± 0.01 |
| CS-B01 F3 | | -0.25 ± 0.02 | -0.21 ± 0.02 | -0.23 ± 0.03 | -0.29 ± 0.02 | -0.25 ± 0.04 |
| CS-T01 F3 | | -0.02 ± 0.03 | -0.05 ± 0.03 | 0.05 ± 0.01 | 0.10 ± 0.02 | 0.03 ± 0.02 |

BW boll weight in grams, *LY* lint yield in kg ha⁻¹, Upper half mean in mm, Uniformity index in Percentage, *STG* Strength in kN m kg⁻¹, *EL* Elongation in percentage, *MIC* Micronaire values

hybrids had higher LP and lower MIC; whereas CS-T04/DP 90 F₂ hybrids had heavier BW, higher LY, greater UHM fiber length and STG. CS-B04 hybrids with each of the five cultivars had greater LP. CS-B04/SG 747 F₂ hybrids had greater LP and MIC; whereas, CS-T04/SG 747 F₂ hybrids had heavier BW, more LY, longer UHM fiber length, and greater fiber UI. CS-B04/PSC 355 F₂ hybrids had higher LP

and heavier BW: whereas CS-T04/PSC 355 F₂ hybrids had longer UHM length, greater UI, and STG. CS-B04/ST 474 F₂ hybrids had higher LP, heavier BW, and longer UHM fiber length; whereas CS-T04/ST 474 hybrids had longer UHM length. CS-B04/FM 966 F₂ hybrids had higher LP and heavier BW; whereas, CS-T04/FM 966 hybrids had greater fiber UI, STG, and EL.

Table 4 Comparison of predicted F₂ and F₃ mean effects and standard errors for eight traits (lint in percentage) for five cultivar crosses with Chromosome 04, expressed as deviations from population mean

| Male parent | Pop mean | DP90 Mean \pm SE | SG747 Mean \pm SE | PSC355 Mean \pm SE | ST474 Mean \pm SE | FM966 \pm SE Mean \pm SE |
|-------------|----------|-----------------------|------------------------|-------------------------|------------------------|---------------------------------|
| LP | 38.28 | | | | | |
| 2010 | | | | | | |
| TM-1 | | -0.57 ± 0.05 | 0.63 ± 0.15 | -0.55 ± 0.08 | 1.19 ± 0.06 | 0.070.04 |
| CS-B04 F2 | | -0.52 ± 0.06 | 0.99 ± 0.13 | 0.64 ± 0.10 | 2.05 ± 0.08 | 1.28 ± 0.10 |
| CS-T04 F2 | | -1.34 ± 0.07 | -0.67 ± 0.13 | -0.75 ± 0.10 | 0.07 ± 0.09 | -0.43 ± 0.11 |
| 2011 | | | | | | |
| TM-1 | | -0.70 ± 0.09 | 0.09 ± 0.08 | -0.43 ± 0.07 | 0.39 ± 0.09 | 0.27 ± 0.08 |
| CS-B04 F3 | | -0.58 ± 0.13 | 1.55 ± 0.058 | 0.21 ± 0.11 | 0.64 ± 0.15 | 1.12 ± 0.11 |
| CS-T04 F3 | | -1.39 ± 0.11 | -1.13 ± 0.06 | -0.92 ± 0.12 | -0.03 ± 0.14 | -0.83 ± 0.13 |
| BW | 5.07 | | | | | |
| 2010 | | | | | | |
| TM-1 | | 0.41 ± 0.02 | 0.20 ± 0.03 | 0.09 ± 0.03 | 0.17 ± 0.02 | 0.75 ± 0.04 |
| CS-B04 F2 | | 0.06 ± 0.04 | 0.03 ± 0.03 | 0.20 ± 0.03 | 0.12 ± 0.02 | 0.62 ± 0.04 |
| CS-T04 F2 | | 0.15 ± 0.02 | 0.16 ± 0.04 | 0.03 ± 0.02 | -0.12 ± 0.03 | 0.39 ± 0.04 |
| 2011 | | | | | | |
| TM-1 | | 0.22 ± 0.03 | 0.15 ± 0.02 | 0.09 ± 0.03 | 0.09 ± 0.06 | 0.60 ± 0.03 |
| CS-B04 F3 | | 0.03 ± 0.03 | -0.03 ± 0.04 | -0.26 ± 0.02 | 0.06 ± 0.02 | 0.22 ± 0.05 |
| CS-T04 F3 | | 0.12 ± 0.03 | 0.28 ± 0.04 | 0.11 ± 0.02 | -0.11 ± 0.03 | 0.36 ± 0.04 |
| LY | 1001 | | | | | |
| 2010 | | | | | | |
| TM-1 | | 80 ± 22 | 235 ± 26 | 70 ± 33 | 121 ± 27 | 21 ± 0 |
| CS-B04 F2 | | 4 ± 20 | -5 ± 16 | 132 ± 16 | 34 ± 18 | 20 ± 0 |
| CS-T04 F2 | | 67 ± 17 | 127 ± 13 | 157 ± 22 | 11 ± 21 | 21 ± 0 |
| 2011 | | | | | | |
| TM-1 | | -10 ± 19 | -3 ± 13 | -120 ± 24 | 50 ± 20 | 9 ± 0 |
| CS-B04 F3 | | -90 ± 27 | 15 ± 24 | 48 ± 16 | 16 ± 21 | 33 ± 1 |
| CS-T04 F3 | | 84 ± 21 | 126 ± 20 | 91 ± 15 | 4 ± 9 | 20 ± 0 |
| UHM | 28.2 | | | | | |
| 2010 | | | | | | |
| TM-1 | | 0.06 ± 0.06 | 0.02 ± 0.04 | 0.0 ± 20.06 | -0.40 ± 0.07 | 0.60 ± 0.08 |
| CS-B04 F2 | | 0.68 ± 0.07 | -0.11 ± 0.13 | 0.04 ± 0.08 | 0.67 ± 0.18 | 0.76 ± 0.06 |
| CS-T04 F2 | | 0.82 ± 0.03 | 0.44 ± 0.08 | 0.40 ± 0.05 | 0.30 ± 0.06 | 0.64 ± 0.06 |
| 2011 | | | | | | |
| TM-1 | | 0.02 ± 0.06 | 0.02 ± 0.11 | 0.18 ± 0.06 | -0.09 ± 0.07 | 0.20 ± 0.05 |
| CS-B04 F3 | | 0.43 ± 0.08 | -0.29 ± 0.07 | -0.06 ± 0.04 | 0.07 ± 0.05 | 0.05 ± 0.05 |
| CS-T04 F3 | | 0.15 ± 0.05 | 0.25 ± 0.07 | 0.1 ± 00.06 | -0.27 ± 0.05 | 0.77 ± 0.11 |
| UI | 83.4 | | | | | |
| 2010 | | | | | | |
| TM-1 | | -0.18 ± 0.09 | 0.28 ± 0.06 | 0.58 ± 0.06 | -0.03 ± 0.07 | 0.42 ± 0.085 |
| CS-B04 F2 | | -0.59 ± 0.10 | -0.12 ± 0.09 | -0.02 ± 0.07 | -0.26 ± 0.22 | 0.16 ± 0.08 |
| CS-T04 F2 | | 0.22 ± 0.07 | 0.74 ± 0.07 | 0.74 ± 0.06 | 0.39 ± 0.07 | 0.61 ± 0.09 |
| 2011 | | | | | | |

Table 4 continued

| Male parent | Pop mean | DP90 Mean \pm SE | SG747 Mean \pm SE | PSC355 Mean \pm SE | ST474 Mean \pm SE | FM966 \pm SE Mean \pm SE |
|-------------|----------|-----------------------|------------------------|-------------------------|------------------------|---------------------------------|
| TM-1 | | -0.14 ± 0.09 | 0.04 ± 0.04 | 0.12 ± 0.06 | 0.21 ± 0.07 | 0.09 ± 0.06 |
| CS-B04 F3 | | 0.21 ± 0.12 | 0.06 ± 0.08 | 0.20 ± 0.09 | 0.03 ± 0.11 | 0.10 ± 0.11 |
| CS-T04 F3 | | 0.06 ± 0.06 | 0.23 ± 0.08 | 0.33 ± 0.08 | -0.11 ± 0.04 | 0.68 ± 0.11 |
| STG | 324.8 | | | | | |
| 2010 | | | | | | |
| TM-1 | | 8.8 ± 1.2 | -11.5 ± 1.8 | -2.7 ± 1.3 | -7.8 ± 1.7 | 30.9 ± 1.0 |
| CS-B04 F2 | | -15.9 ± 1.6 | -8.1 ± 0.9 | -4.6 ± 1.7 | -15.9 ± 2.8 | 7.2 ± 1.0 |
| CS-T04 F2 | | 3.2 ± 1.0 | -16.9 ± 1.5 | 7.7 ± 1.5 | -10.8 ± 1.6 | 29.1 ± 1.7 |
| 2011 | | | | | | |
| TM-1 | | 9.7 ± 2.0 | -16.2 ± 0.9 | -2.6 ± 2.4 | -4.6 ± 2.9 | 30.4 ± 1.8 |
| CS-B04 F3 | | -4.0 ± 1.7 | -23.3 ± 2.0 | -6.9 ± 1.4 | -17.2 ± 1.6 | 6.9 ± 2.0 |
| CS-T04 F3 | | 3.4 ± 1.3 | -9.3 ± 1.6 | 5.7 ± 2.9 | -4.5 ± 1.2 | 25.8 ± 3.0 |
| EL | 7.04 | | | | | |
| 2010 | | | | | | |
| TM-1 | | -0.11 ± 0.03 | -0.2 ± 10.03 | 0.30 ± 0.03 | -0.17 ± 0.03 | -0.29 ± 0.02 |
| CS-B04 F2 | | -0.10 ± 0.04 | -0.12 ± 0.02 | 0.41 ± 0.04 | -0.23 ± 0.03 | -0.57 ± 0.03 |
| CS-T04 F2 | | -0.17 ± 0.05 | -0.08 ± 0.02 | 0.39 ± 0.03 | -0.08 ± 0.04 | -0.14 ± 0.04 |
| 2011 | | | | | | |
| TM-1 | | -0.04 ± 0.02 | 0.05 ± 0.04 | -0.01 ± 0.06 | -0.06 ± 0.03 | -0.13 ± 0.03 |
| CS-B04 F3 | | -0.02 ± 0.02 | -0.14 ± 0.04 | 0.22 ± 0.03 | -0.13 ± 0.02 | -0.17 ± 0.03 |
| CS-T04 F3 | | -0.01 ± 0.03 | 0.07 ± 0.03 | 0.14 ± 0.02 | -0.07 ± 0.02 | -0.2 ± 10.02 |
| MIC | 4.99 | | | | | |
| 2010 | | | | | | |
| TM-1 | | -0.06 ± 0.02 | -0.19 ± 0.03 | 0.07 ± 0.03 | 0.07 ± 0.03 | 0.09 ± 0.02 |
| CS-B04 F2 | | -0.34 ± 0.03 | -0.27 ± 0.02 | 0.24 ± 0.02 | -0.06 ± 0.02 | 0.14 ± 0.02 |
| CS-T04 F2 | | -0.05 ± 0.04 | -0.04 ± 0.03 | 0.24 ± 0.03 | -0.09 ± 0.04 | 0.04 ± 0.02 |
| 2011 | | | | | | |
| TM-1 | | -0.03 ± 0.02 | 0.05 ± 0.03 | 0.08 ± 0.02 | -0.12 ± 0.03 | 0.01 ± 0.01 |
| CS-B04 F3 | | -0.08 ± 0.02 | 0.00 ± 0.03 | 0.03 ± 0.02 | 0.03 ± 0.01 | 0.08 ± 0.01 |
| CS-T04 F3 | | 0.12 ± 0.03 | -0.11 ± 0.04 | 0.19 ± 0.03 | 0.12 ± 0.01 | 0.08 ± 0.03 |

BW boll weight in grams, *LY* lint yield in kg ha⁻¹, Upper half mean in mm, Uniformity index in Percentage, *STG* Strength in kN m kg⁻¹, *EL* Elongation in percentage, *MIC* Micronaire values

Predicted genotypic effects of chromosome 18 hybrids

CS-B18/DP 90 F₂ hybrids had higher LP, stronger fiber STG, and greater EL; whereas, CS-T18/DP 90 hybrids had higher LY, longer UHM length, and lower MIC. CS-B18/SG 747 F₂ hybrids had higher LP and heavier BW; whereas, CS-T18/SG 747 hybrids had longer UHM length, greater fiber UI and EL. CS-B18/PSC 355 F₂ hybrids had higher LP, heavier BW, longer UHM length, and greater EL; whereas, CS-T18/PSC 355 hybrids had

greater LY and fiber with higher UI. CS-B18/ST 474 F₂ hybrids had higher LP, heavier BW, and higher LY; whereas, CS-T18/ST 474 hybrids had greater UI and lower MIC. CS-B18/FM 966 F₂ hybrids had higher LP, heavier BW, with stronger fiber; whereas, CS-T18/FM 966 hybrids had higher fiber UI and lower MIC (Table 5).

Discussion

Overall, this study allowed for several different types of meaningful mean comparisons. Comparing CSL

Table 5 Comparison of predicted F₂ and F₃ mean effects and standard errors for eight traits (lint in percentage) for five cultivar crosses with Chromosome 18, expressed as deviations from population mean

| Male parent | Pop mean | DP90 Mean \pm SE | SG747 Mean \pm SE | PSC355 Mean \pm SE | ST474 Mean \pm SE | FM966 Mean \pm SE |
|-------------|----------|-----------------------|------------------------|-------------------------|------------------------|------------------------|
| LP | 38.28 | | | | | |
| 2010 | | | | | | |
| TM-1 | | -0.57 ± 0.05 | 0.63 ± 0.15 | -0.55 ± 0.08 | 1.19 ± 0.06 | 0.07 ± 0.04 |
| CS-B18 F2 | | -0.53 ± 0.11 | 1.95 ± 0.13 | 1.48 ± 0.10 | 2.3 ± 30.07 | 0.48 ± 0.07 |
| CS-T18 F2 | | -1.59 ± 0.09 | 0.29 ± 0.09 | -0.46 ± 0.08 | -0.10 ± 0.09 | -0.17 ± 0.07 |
| 2011 | | | | | | |
| TM-1 | | -0.70 ± 0.09 | 0.09 ± 0.08 | -0.43 ± 0.07 | 0.39 ± 0.09 | 0.27 ± 0.08 |
| CS-B18 F3 | | -0.70 ± 0.08 | 1.10 ± 0.15 | 1.30 ± 0.12 | 1.47 ± 0.10 | 0.26 ± 0.13 |
| CS-T18 F3 | | -1.15 ± 0.07 | -0.75 ± 0.15 | -0.24 ± 0.07 | 0.34 ± 0.10 | 0.71 ± 0.10 |
| BW | 5.07 | | | | | |
| 2010 | | | | | | |
| TM-1 | | 0.41 ± 0.02 | 0.20 ± 0.03 | 0.09 ± 0.03 | 0.17 ± 0.02 | 0.75 ± 0.04 |
| CS-B18 F2 | | 0.23 ± 0.04 | 0.03 ± 0.03 | 0.09 ± 0.03 | 0.05 ± 0.04 | 0.61 ± 0.03 |
| CS-T18 F2 | | -0.13 ± 0.03 | -0.34 ± 0.04 | -0.56 ± 0.04 | -0.48 ± 0.02 | 0.46 ± 0.03 |
| 2011 | | | | | | |
| TM-1 | | 0.22 ± 0.03 | 0.15 ± 0.02 | 0.09 ± 0.03 | 0.09 ± 0.06 | 0.60 ± 0.03 |
| CS-B18 F3 | | -0.01 ± 0.04 | 0.02 ± 0.04 | -0.19 ± 0.03 | -0.32 ± 0.04 | 0.37 ± 0.04 |
| CS-T18 F3 | | -0.20 ± 0.03 | -0.16 ± 0.03 | -0.56 ± 0.04 | -0.39 ± 0.03 | 0.05 ± 0.04 |
| LY | 1001 | | | | | |
| 2010 | | | | | | |
| TM-1 | | 80 ± 22 | 235 ± 26 | 7 ± 033 | 121 ± 27 | 21 ± 0 |
| CS-B18 F2 | | -112 ± 25 | -125 ± 17 | -80 ± 14 | -50 ± 14 | 12 ± 0 |
| CS-T18 F2 | | -25 ± 21 | -147 ± 18 | -5 ± 22 | -175 ± 10 | 36 ± 0 |
| 2011 | | | | | | |
| TM-1 | | -10 ± 19 | -3 ± 13 | -120 ± 24 | 50 ± 20 | 9 ± 0 |
| CS-B18 F3 | | -62 ± 15 | -3 ± 16 | 53 ± 14 | -5 ± 23 | 19 ± 1 |
| CS-T18 F3 | | -17 ± 20 | -89 ± 19 | -31 ± 22 | 23 ± 14 | 15 ± 0 |
| UHM | 28.2 | | | | | |
| 2010 | | | | | | |
| TM-1 | | 0.06 ± 0.06 | 0.02 ± 0.04 | 0.02 ± 0.06 | -0.40 ± 0.07 | 0.60 ± 0.08 |
| CS-B18 F2 | | 0.16 ± 0.07 | -0.05 ± 0.07 | -0.13 ± 0.04 | -0.51 ± 0.05 | 0.50 ± 0.04 |
| CS-T18 F2 | | 0.72 ± 0.06 | 0.36 ± 0.07 | -0.27 ± 0.05 | -0.20 ± 0.05 | 0.50 ± 0.06 |
| 2011 | | | | | | |
| TM-1 | | 0.0 ± 20.06 | 0.02 ± 0.11 | 0.18 ± 0.06 | -0.09 ± 0.07 | 0.20 ± 0.05 |
| CS-B18 F3 | | -0.03 ± 0.09 | -0.34 ± 0.08 | -0.19 ± 0.08 | -0.78 ± 0.08 | 0.18 ± 0.06 |
| CS-T18 F3 | | 0.33 ± 0.05 | 0.28 ± 0.07 | -0.11 ± 0.04 | -0.01 ± 0.10 | -0.24 ± 0.05 |
| UI | 83.4 | | | | | |
| 2010 | | | | | | |
| TM-1 | | -0.18 ± 0.09 | 0.28 ± 0.06 | 0.58 ± 0.06 | -0.03 ± 0.07 | 0.42 ± 0.08 |
| CS-B18 F2 | | -0.41 ± 0.07 | -0.38 ± 0.05 | -0.49 ± 0.04 | -0.47 ± 0.07 | -0.18 ± 0.06 |
| CS-T18 F2 | | -0.44 ± 0.08 | 0.33 ± 0.11 | 0.10 ± 0.09 | -0.51 ± 0.08 | 0.23 ± 0.09 |
| 2011 | | | | | | |
| TM-1 | | -0.14 ± 0.09 | 0.04 ± 0.04 | 0.12 ± 0.06 | 0.21 ± 0.07 | 0.09 ± 0.06 |

Table 5 continued

| Male parent | Pop mean | DP90 Mean \pm SE | SG747 Mean \pm SE | PSC355 Mean \pm SE | ST474 Mean \pm SE | FM966 Mean \pm SE |
|-------------|----------|-----------------------|------------------------|-------------------------|------------------------|------------------------|
| CS-B18 F3 | | -0.31 ± 0.12 | -0.41 ± 0.14 | -0.32 ± 0.10 | -0.49 ± 0.11 | -0.01 ± 0.07 |
| CS-T18 F3 | | -0.19 ± 0.05 | 0.05 ± 0.04 | 0.04 ± 0.06 | -0.09 ± 0.10 | -0.18 ± 0.07 |
| STG | 324.8 | | | | | |
| 2010 | | | | | | |
| TM-1 | | 8.8 ± 1.2 | -11.5 ± 1.8 | -2.7 ± 1.3 | -7.8 ± 1.7 | 30.9 ± 1.0 |
| CS-B18 F2 | | 7.6 ± 2.4 | -15.2 ± 1.9 | 2.8 ± 1.7 | -7.8 ± 1.4 | 34.7 ± 1.7 |
| CS-T18 F2 | | 4.5 ± 1.8 | -10.7 ± 1.3 | -2.1 ± 1.7 | -2.8 ± 1.8 | 23.5 ± 0.9 |
| 2011 | | | | | | |
| TM-1 | | 9.7 ± 2.0 | -16.2 ± 0.9 | -2.6 ± 2.4 | -4.6 ± 2.9 | 30.4 ± 1.8 |
| CS-B18 F3 | | 11.4 ± 1.1 | -2.2 ± 1.7 | 0.6 ± 1.3 | -11.1 ± 1.5 | 30.7 ± 2.1 |
| CS-T18 F3 | | 5.7 ± 2.9 | -3.0 ± 3.2 | 3.3 ± 1.5 | -9.1 ± 1.8 | 25.6 ± 2.6 |
| EL | 7.04 | | | | | |
| 2010 | | | | | | |
| TM-1 | | -0.11 ± 0.03 | -0.21 ± 0.03 | 0.30 ± 0.03 | -0.17 ± 0.03 | -0.29 ± 0.02 |
| CS-B18 F2 | | -0.05 ± 0.04 | 0.07 ± 0.05 | 0.40 ± 0.04 | -0.16 ± 0.04 | -0.24 ± 0.04 |
| CS-T18 F2 | | -0.39 ± 0.04 | 0.13 ± 0.04 | 0.27 ± 0.03 | -0.12 ± 0.05 | -0.18 ± 0.06 |
| 2011 | | | | | | |
| TM-1 | | -0.04 ± 0.02 | 0.05 ± 0.04 | -0.01 ± 0.06 | -0.06 ± 0.03 | -0.13 ± 0.03 |
| CS-B18 F3 | | 0.02 ± 0.02 | 0.15 ± 0.03 | 0.14 ± 0.04 | 0.04 ± 0.03 | -0.03 ± 0.03 |
| CS-T18 F3 | | -0.21 ± 0.03 | 0.03 ± 0.03 | 0.15 ± 0.02 | -0.13 ± 0.02 | -0.20 ± 0.04 |
| MIC | 4.99 | | | | | |
| 2010 | | | | | | |
| TM-1 | | -0.06 ± 0.02 | -0.19 ± 0.03 | 0.07 ± 0.03 | 0.07 ± 0.03 | 0.09 ± 0.02 |
| CS-B18 F2 | | 0.12 ± 0.03 | 0.23 ± 0.02 | 0.42 ± 0.01 | 0.32 ± 0.03 | 0.40 ± 0.03 |
| CS-T18 F2 | | -0.20 ± 0.03 | 0.11 ± 0.02 | 0.36 ± 0.03 | -0.05 ± 0.02 | 0.19 ± 0.02 |
| 2011 | | | | | | |
| TM-1 | | -0.03 ± 0.02 | 0.05 ± 0.03 | 0.08 ± 0.02 | -0.12 ± 0.03 | 0.01 ± 0.01 |
| CS-B18 F3 | | -0.04 ± 0.02 | 0.27 ± 0.02 | 0.15 ± 0.04 | 0.24 ± 0.02 | 0.22 ± 0.03 |
| CS-T18 F3 | | 0.01 ± 0.03 | -0.06 ± 0.03 | 0.10 ± 0.03 | -0.02 ± 0.04 | 0.07 ± 0.03 |

BW boll weight in grams, LY lint yield in kg ha^{-1} , Upper half mean in mm, Uniformity index in Percentage, STG Strength in kN m kg^{-1} , EL Elongation in percentage, MIC Micronaire values

mean performance to commercial cultivars provided an estimation of agronomic and fiber quality performance of CSLs per se. Comparing CSLs and TM-1 for each substituted chromosome allowed individual effects of chromosomes from *G. hirsutum*, *G. barbadense*, and *G. tomentosum* to be compared within a near isochromosomal, *G. hirsutum* genetic background. Compared to commercial cultivars, CSLs produced lower LP and LY but produced similar fiber quality properties. SG 747 and ST 474 had the highest LP among parents and both CS-B01 and CS-T01 hybrids with these two cultivars had the greatest LP

among hybrids, probably reflecting the higher LP of these two cultivars.

Considering single chromosome comparisons (within an isochromosomal *G. hirsutum* genetic background) relative to *G. hirsutum*, *G. barbadense* and *G. tomentosum* chromosomes decreased or produced similar BW and LY for chromosomes 1, 4, and 18. Interestingly, *G. barbadense* and *G. tomentosum* chromosomes produced opposite effects for LP. For chromosomes 4 and 18, *G. barbadense* chromosomes increased LP while *G. tomentosum* decreased LP. For chromosome 1, *G. barbadense* decreased LP while *G.*

tomentosum increased LP. In terms of fiber quality traits, single chromosome comparisons relative to *G. hirsutum* showed positive and negative effects of single chromosomes. *G. barbadense* and *G. tomentosum* chromosome 4 increased UHM fiber length, while for chromosome 18 both species chromosome substitutions decreased UHM and UI. Substituted chromosome 18 from both species provided similar or increased fiber STG relative to *G. hirsutum*. Opposite effects of *G. barbadense* and *G. tomentosum* chromosomes for chromosome 1 and 4 were identified for UI and STG. Most notably, *G. barbadense* chromosome 4 significantly decreased STG. There was no single chromosome from the three species that was superior for all traits in crosses.

Comparing chromosome 1 F₂ hybrids among the three species for LP ranks were *tomentosum* > *hirsutum* > *barbadense*. LY was cultivar cross specific with *G. barbadense* being more favorable with DP 90 and PSC 355 and *G. tomentosum* with SG 747 and ST 474. BW ranked *hirsutum* > *barbadense* > *tomentosum*. Fiber UHM, UI fiber uniformity, and MIC ranked *barbadense* > *hirsutum* > *tomentosum*. The greatest STG was in FM 966 hybrids with all three species hybrids about equal.

Comparing chromosome 4 F₂ hybrids among the three species, LP ranked *barbadense* > *tomentosum* > *hirsutum*. BW ranked *hirsutum* > *tomentosum* > *barbadense* for hybrids with DP 90 and SG 747 and ranked *barbadense* > *hirsutum* > *tomentosum* for hybrids with PSC 355. Hybrids with *G. hirsutum* produced more LY with DP 90, SG 747, and ST 474; whereas for hybrid with PSC 355 LY ranks were *tomentosum* > *barbadense* > *hirsutum*. *G. tomentosum* hybrids with DP 90, SG 747, and PSC 355 were greater than *barbadense* hybrids, and *barbadense* hybrids with ST 474 and FM 966 were greater than *tomentosum* hybrids for fiber UHM length. For fiber UI ranks were *tomentosum* > *barbadense* > *hirsutum*. Hybrids with FM 966 and *hirsutum* and *tomentosum* increased STG more than any other hybrids. MIC was reduced in *G. barbadense* hybrids with DP 90 and SG 747 and increased in both *G. barbadense* and *G. tomentosum* hybrids with PSC 355.

Comparing chromosome 18 F₂ hybrids among the three species for LP ranks were *barbadense* > *tomentosum* or *hirsutum*. BW generally ranked *hirsutum* > *barbadense* > *tomentosum*. LY of all hybrids with *G. hirsutum*, except FM 966, were greater than

with all others. UHM could be increased with *G. tomentosum* hybrids with DP 90 and SG 747 and with any hybrid with FM 966. Hybrids with chromosome 18 had little effect on UI or STG, except STG was increased with any hybrid with FM 966. No major effects were gained for EL or MIC in any hybrids. It is interesting that STG of both hybrids with FM 966 was increased compared with other cultivar hybrids with chromosome 18 hybrids.

Results from our additive-dominance (AD) model analysis (Jenkins et al. 2017) showed that both additive and dominance genetic effects between alleles from five cultivars and these CSL from the three tetraploid species were significant for most agronomic and fiber traits measured. These results were consistent with the predicted F₂ and F₃ effects as shown in Tables 2, 3, and 4 of this study. The results in Tables 3, 4, and 5 showed predicted F₂ and F₃ mean effects were highly consistent with a few exceptions, indicating that breeders should be able to use these crosses as base populations to improve selective traits. It is also possible that epistatic effects among different loci impact yield and fiber traits (McCarty et al. 2004a, b) however, with the current data structures we were unable to quantify these effects. Association mapping techniques using recombinant inbred lines derived from these populations from the three tetraploid species will be a desirable approach to identifying epistatic effects.

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Compliance with ethical standards

Conflict of interest None.

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